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# FLUX OF LARVAL FISHES ACROSS FRONTAL BOUNDARIES: EXAMPLES FROM THE MISSISSIPPI RIVER PLUME FRONT AND THE WESTERN GULF STREAM FRONT IN WINTER

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## ABSTRACT

Boundaries between water masses, frontal zones, are neither static nor impervious: they are dynamic. There is exchange of water across frontal zones and, as a consequence, there is flux of biota. The spatial distribution of larval gulf and Atlantic menhaden (*Brevoortia patronus* and *B. tyrannus*), and spot (*Leiostomus xanthurus*), presumed indicators of larval fish assemblages in and about two well defined, but vastly different frontal zones, serve as examples of the flux of larval fishes across water-mass boundaries. Across the Mississippi River plume front in the Gulf of Mexico and the western Gulf Stream front in the southeastern Atlantic bight of the United States, mixing and stirring can account for flux of larval fishes. The consequences of flux for the larvae of these indicator species is their shoreward transport, or the reciprocal, their expatriation from coastal populations.

The water masses that constitute the world's oceans are sometimes bounded by frontal zones, typically regarded as the surface expression of sharp gradients in physical properties. Frontal zones often are areas of enhanced primary productivity, aggregations of plankton, and elevated abundances of nekton (Bowman and Iverson, 1978; Owen, 1981; Le Fèvre, 1986). Enhanced primary production results mainly from the injection of nutrients into surface water from below through upwelling associated with frontal dynamics, although in the specific case of riverine and estuarine fronts it may result from horizontal and vertical mixing of nutrient-rich, riverine effluent with continental-shelf or oceanic waters (Lohrenz et al., 1990). Aggregation of plankton results from its accumulation through horizontal hydrodynamic convergence (Kingsford, 1990). Nekton is at times more abundant in frontal zones either because of an edge effect, i.e., animals accumulate as they encounter and remain within a preferred physical environment (temperature or salinity) that is bounded by the front, or because animals actively seek and find the enhanced feeding environments associated with these areas.

Frontal zones encompass water masses as well as the plankton that they contain, but how tight are these boundaries? Physical processes operate to exchange water between water masses, and as a result, there is flux of biota across frontal zones. Exchange processes and the consequential flux of phyto- and zooplankton are well documented by Wroblewski and Hofmann (1989). Translocation of larval fishes across frontal zones is more equivocal. On Georges Bank in the western North Atlantic north of Cape Hatteras, larval fishes move onto the bank with intruding Gulf Stream water, sometimes becoming mixed with local larval fish assemblages as the result of turbulence, but at other times displacing local assemblages (Colton and Temple, 1961; Flierl and Wroblewski, 1985). Cowen et al. (this volume) invoke this sort of dynamic activity to explain the composition of ichthyoplankton in the middle Atlantic bight south of Georges Bank. In contrast, there is little evidence of flux of larval fishes across the inner, mid-, and shelf-break fronts on the Bering Sea shelf, even though processes of physical exchange are at work (Walsh and McRoy, 1986). Fish larvae accumulate within plume, shelf-break, tidal, and western boundary fronts throughout the world's oceans (Pingree et al., 1974; Sakamoto and Tanaka, 1986; Sabatès, 1990a, 1990b; Sabatès and Mas, 1990), but where appropriately examined for flux, they appear to be retained

within frontal zones (Kiørboe et al., 1988; Iwatsuki et al., 1989; Nakata, 1989). In similar fashion, larval fishes accumulate along, but remain segregated within, juxtaposed water masses, in an estuarine front in the Gulf of St. Lawrence (Côté et al., 1986).

Neither has the flux of larvae across fronts been demonstrated where elevated densities of fish eggs and larvae result from directed spawning within these features. The most convincing evidence of spawning within frontal zones exists for the northern subpopulation of *Engraulis mordax* in the Columbia River plume off Oregon and Washington (Richardson, 1981) and *Sardinops melanosticta* in the western edge of the Kuroshio current, a western boundary current (Tsujita, 1957; Funakoshi and Yanagibashi, 1983).

The purpose here is to examine, for examples of flux across frontal zones, the spatial distribution of the larvae of three indicator species (sensu Bratkovich, 1988) that are associated with two well defined frontal zones, then to attempt to explain observed flux with the physical processes that operate in the exchange of water between water masses. First, I will review briefly the early life histories of these species, the processes of physical exchange, and the most germane of these processes as they might operate in the flux of larval fishes within and across the two specific frontal zones. The perspective will be biological, i.e., a view of the application of physical processes to the understanding of the distribution of larval fishes. I will not attempt to quantify the flux of fish larvae, but simply will illustrate flux with examples, then briefly discuss probable causes and possible consequences.

Specifically, I will examine the horizontal distribution of gulf and Atlantic menhaden (*Brevoortia patronus* and *B. tyrannus*) and spot (*Leiostomus xanthurus*) in, and about the Mississippi River plume front in the northern Gulf of Mexico and the western Gulf Stream front off Onslow Bay in the northern reaches of the southeastern Atlantic bight of the United States. These species share generally similar early life histories (Hata, 1985; Mercer, 1987; Powell, 1989) and are associated with the two frontal zones, although for different reasons. The two frontal zones differ in their spatial scale, physical attributes, and dynamics (Stommel, 1965; Wright and Coleman, 1971).

For the purpose of this discussion, I will use the rather broad definition of Bowman (1978) in defining a frontal zone: "an oceanic surface front is the sea surface manifestation of a sharp boundary zone between adjacent water masses of dissimilar properties."

#### INDICATOR SPECIES

The larvae of *B. tyrannus*, *B. patronus*, and *L. xanthurus* are associated with the Mississippi River plume front in the northern Gulf of Mexico and the western Gulf Stream front in the Atlantic. In the Gulf of Mexico, *B. patronus* and *L. xanthurus* spawn across the northern Gulf (Nelson and Ahrenholz, 1986; Ahrenholz et al., 1987; Hata, 1985). In early winter, older *B. patronus* move toward the Mississippi River Delta, the focus of spawning (Ahrenholz, 1981). Larvae of both species are distributed on the shelf across the northern Gulf (Cowan and Shaw, 1988; Shaw and Drullinger, 1990), with highest abundance just south of the Mississippi River delta (Sogard et al., 1987). There is presently no indication that spawning of either species is associated exclusively with the Mississippi River plume or its front. Larvae occur in greatest abundance within the frontal zone because they accumulate there as a result of frontal convergence (Govoni et al., 1989; Govoni and Grimes, 1992).

In the Atlantic, adult *B. tyrannus* and *L. xanthurus* migrate seasonally, zonally, and meridionally to spawn (Nicholson, 1978; Mercer, 1987; Norcross and Bodolus, 1991). North of Cape Hatteras, *B. tyrannus* spawns near shore or even within large estuaries (Nelson et al., 1977, Bourne and Govoni, 1988), but the bulk of spawning is primarily offshore from Delaware Bay to the Charleston Bump, a topographical rise on the continental slope at 32°N latitude (Kendall and Reintjes, 1975; Judy and Lewis, 1983). *Leiostomus xanthurus* spawns on the shelf, primarily south of Cape Hatteras (Mercer, 1987; Norcross and Bodolus, 1991). Smaller and younger larvae of both species occur offshore, and there is a gradient of increasing size and age of larvae toward the coast (Judy and Lewis, 1983; Lewis and Judy, 1983; Warlen and Chester, 1985; Warlen, 1988, 1992; Flores-Coto and Warlen, 1993). The largest and oldest larvae enter estuaries from November until April; peak ingress is in late February and March (Hettler and Chester, 1990; Warlen and Burke, 1990). Juveniles are not caught in appreciable numbers in coastal or shelf waters, a fact that leads to the belief that larvae complete transformation and spend the remainder of their first year in estuaries and sounds (Ahrenholz et al., 1989; Mercer, 1987).

The precise focus of spawning of either species on the shelf south of Cape Hatteras is uncertain, yet the offshore-inshore gradient in the age structure of populations of larvae, coupled with attempts to spawn adults in the laboratory, has led to the conclusion that *B. tyrannus* and *L. xanthurus* spawn primarily during winter in association with the Gulf Stream front. Marginal spawning may begin in the fall at mid-shelf locations, but progresses offshore as shelf waters cool with the season (Flores-Coto and Warlen, 1993; Warlen, 1992). Artificially induced spawning of both species in the laboratory is successful only at temperatures of 16 to 25°C (Hettler, 1981; Hettler and Powell, 1981). During winter, water of these temperatures are found only offshore, near or in the Gulf Stream front (Checkley et al., 1988). In a singular report, Reintjes (1969) observed "hundreds of thousands of eggs of *B. tyrannus* in a series of 10-min plankton tows in an area less than 8 km in diameter, 65 km off New River Inlet." This area, which will be discussed in detail later, lies on the outer shelf in Onslow Bay and is subject to filaments and eddies of the Gulf Stream as well as upwelling (Pietrafesa et al., 1985a).

#### EXCHANGE PROCESSES

Exchange will be regarded here as the resultant of two composite processes that operate through different modes and at different scales: mixing and stirring (Power, 1982; Svendsen, 1986). Mixing is a diffusive process that refers to small scale (< 1 km) turbulence (molecular and eddy diffusion). For example, vertical mixing can occur through entrainment, a process that results when shear between upper and lower water masses increases to the point where small waves break and elements of water from below are injected into the surface layer where they diffuse. Double-diffusive processes that effect mixing by the concerted action of diffusion of physical properties (salt or heat) and small scale horizontal incursions of water (so called "salt-fingering") is another example of mixing. Stirring is an advective process that refers to coherent motions on scales of kilometers and more (i.e., eddies, filaments, and intrusions in the horizontal, upwelling in the vertical). Stirring often acts to sharpen physical gradients, whereas mixing acts to smear these gradients (Svendsen, 1986). The two processes are linked, however; stirring acts to increase surface area contact between two water masses, thereby enhancing mixing (Joyce, 1977). This coupling is apparent from the fact that large scale

spatial variations in the temperature (T) and salinity (S), the T/S signature of water types, will, in time be smoothed by mixing (Stern, 1967).

While fronts separate water masses and are areas of sharp gradients in physical properties, they are also areas of enhanced exchange (Joyce, 1977; Horne et al., 1978; Huthnance, 1981; Houghton and Marra, 1983; Simpson and James, 1986). The two physical processes that effect exchange, however, operate largely along different coordinates because of differences in scale (Lam et al., 1984). Mixing operates mainly in the vertical; stirring in the horizontal. While horizontal mixing occurs, its parameters are difficult to estimate within frontal zones, and it is typically overwhelmed by advection.

#### FRONTAL ZONES

*Mississippi River Plume Front.*—Through controlled flow, the Mississippi River discharges two thirds of its water through the numerous distributaries of the Mississippi Delta (Gunter, 1979). Discharged freshwater produces a buoyant plume of turbid, low salinity water that overrides the saline water of the northern Gulf of Mexico. In winter, plume water is cooler and less saline than shelf water (Govoni et al., 1989). Owing to the typical east-west flow field and to Coriolis deflection, the plume generally veers westward (Chew et al., 1962; Rouse and Coleman, 1976) over a continental shelf that is some 50 km wide (the shelf break begins at the 80 m isobath seaward of the major Mississippi River distributaries [Adams et al., 1987]). Horizontally, plume water is separated from shelf water by a conspicuous and persistent frontal zone (Wright and Coleman, 1971).

The Mississippi River plume front is a large scale (2 to 20 km) frontal zone (Govoni et al., 1989; Lohrenz et al., 1990; Grimes and Finucane, 1991). Sharp, small-scale (1 to 50 m) horizontal discontinuities in physical properties, including turbidity, are often embedded within the large scale frontal zone (Fig. 1), these apparently forming on the ebb of the diurnal tide (Seim et al., 1987) and dissipating on the flood (Grimes and Finucane, 1991; Govoni and Grimes, 1992). Convergence of surface water is apparent along small scale turbidity discontinuities, and there is often evidence of lateral shear (Govoni and Grimes, 1992). Apparent convergence is probably driven by spreading of surface water over shelf water, as well as by pressure gradient forces (Garvine, 1980; Govoni and Grimes, 1992).

Mixing across the Mississippi River plume front is obvious from the distribution of salt. Surface river water within the major distributary passes during winter is relatively fresh with salinities  $<5\text{‰}$ , whereas surface plume water on the shelf is brackish,  $>5$  and  $<30\text{‰}$  (unpubl.; Govoni et al., 1989; Govoni and Grimes, 1992). Mixing results primarily through vertical entrainment, although tidal currents and wind-induced horizontal mixing add to the overall effect (Wright and Coleman, 1971). Turbulent rotor action at the leading edge of turbidity discontinuities such as that described by Luketina and Imberger (1989) is also observable (Govoni and Grimes, 1992). The broad scale of the frontal zone probably results from mixing that operates as the front alternately sharpens then relaxes with the diurnal tidal cycle (Seim et al., 1987; Govoni and Grimes, 1992). Evidence of fresh water from the Mississippi River plume is seen as far west as the Texas shelf (Dinnel and Wiseman, 1986).

Stirring is less obvious, but the sinuous configuration of turbidity discontinuities within the plume's frontal zone (Fig. 1), indicates that stirring through eddy formation is possible. The cumulative effect of mixing and stirring is a short, 2-d residence time of plume water (Lohrenz et al., 1990).

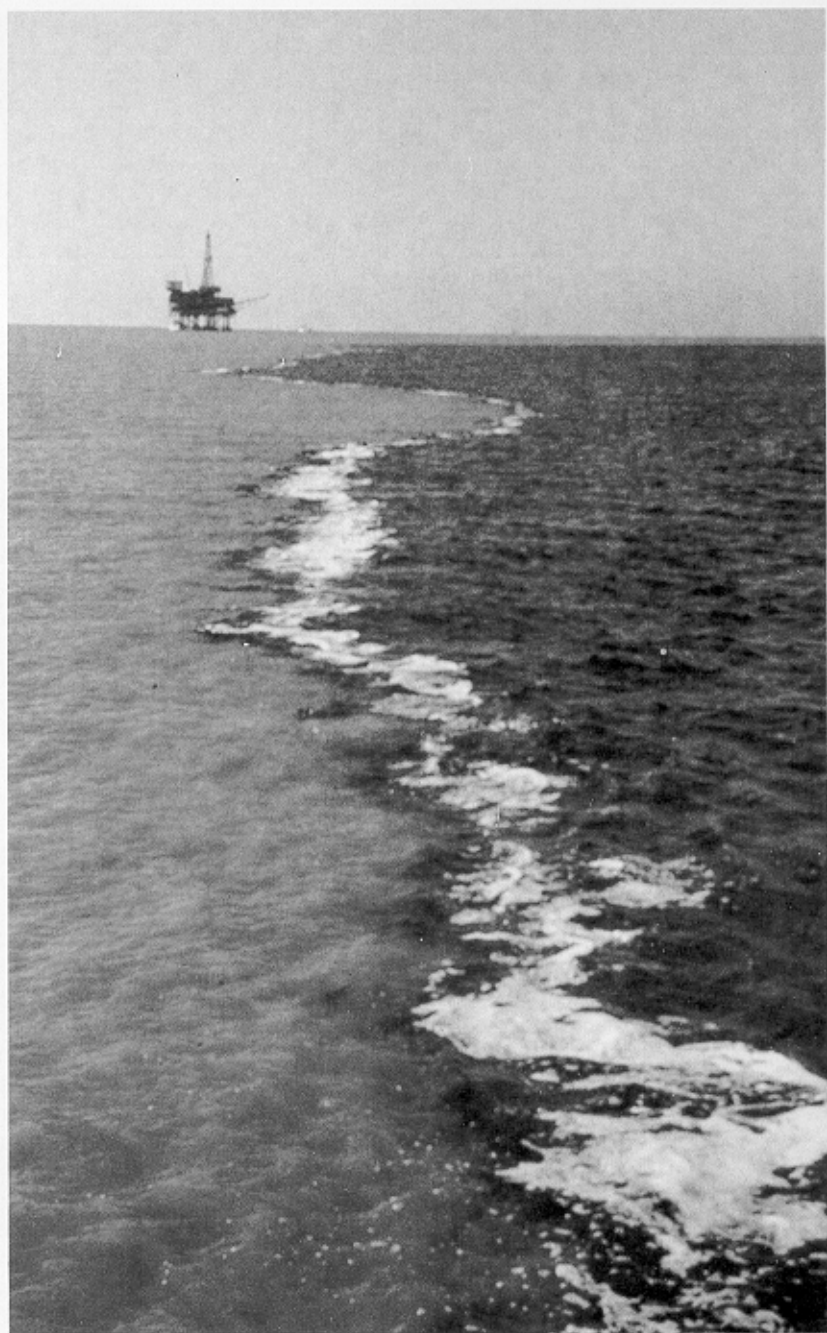


Figure 1. Photograph of a turbidity discontinuity within the Mississippi River plume front (plume water is to the left, shelf water to the right).

*Gulf Stream Front.*—The Gulf Stream (Fig. 2) is one of the most physically dramatic and well studied of all the western boundary currents. Gulf Stream water possesses a distinct T/S signature. In winter, Gulf Stream water has temperatures of 22 to 26°C and salinities of 36.0 and 36.7‰ in the southeastern Atlantic bight



Figure 2. Advanced, very high resolution radiometer infrared image of the southeastern Atlantic bight of the United States, 11 February 1991 (NOAA-11 satellite: the arrow points to the eastward deflection of the Gulf Stream at the "Charleston Bump"; mottled white areas to the far right are clouds). Note the instability of the Gulf Stream front north of the "Charleston Bump."

(Atkinson, 1985; Pietrafesa et al., 1985a). It is not a "river of hot water flowing through the ocean, but a narrow ribbon of high velocity water acting as a boundary that prevents warm Sargasso Sea water from over-flowing cooler inshore water" (Stommel, 1965).

The Gulf Stream front is a pressure gradient between juxtaposed water masses (von Arx et al., 1955); the western edge of this large scale front is the point where the pressure gradient is zero (Stommel, 1965). Temperature, salinity, texture, and sometimes sea-color gradients at the sea surface, typically taken as the western Gulf Stream front, usually coincide with this boundary (Stommel, 1965). Con-

vergence zones are common within the Gulf Stream front (Garvine, 1980). South of Cape Hatteras, along the offshore margin of the southeastern Atlantic bight, the western Gulf Stream front separates shelf water from Sargasso Sea water; north of Cape Hatteras, along the offshore margin of the mid-Atlantic bight, it separates slope water (a mixture of shelf and Gulf Stream water) from Sargasso Sea water (Cowen et al., 1993). Thus, south of Cape Hatteras, Gulf Stream water interacts directly with shelf water (or Carolina Capes water in Onslow Bay), resulting in considerable exchange of shelf and Gulf Stream water (Blanton and Pietrafesa, 1978). Although the Gulf Stream front is sometimes cooler (Stefánsson et al., 1971), the 22°C isotherm typically is located at its western edge (Pietrafesa, 1989).

Another front, the outer-shelf front, exists over the outer continental shelf and shelf break in winter, and while it is inshore of the Gulf Stream front, the two fronts often interact. The outer-shelf front usually is defined by horizontally compressed 18 to 19°C, vertical isotherms (Atkinson et al., 1983; Oey, 1986). The outer-shelf front can merge with, or separate from, the Gulf Stream front, depending upon the position and behavior of the Gulf Stream. Taken as a whole, the outer-shelf and Gulf Stream fronts encompass a band of 18 to 22°C water, 20 to 40 km wide (McClain et al., 1984, 1988), that affords a spawning environment for *B. tyrannus* and *L. xanthurus* (Checkley et al., 1988).

This band of 18 to 22°C water results from the combined action of mixing and stirring. As the Gulf Stream courses northward following the shelf break (Atkinson and Menzel, 1985; Lee et al., 1989), it is deflected eastward by the Charleston Bump (Pietrafesa et al., 1985a). This deflection (Fig. 2) amplifies existing instabilities in the flow of the Gulf Stream resulting in horizontal waves 100 to 300 km long (Pietrafesa et al., 1985a) that propagate northward at speeds of 40 km · d<sup>-1</sup> and transit Onslow Bay every 3 to 10 d (Brooks and Bane, 1983). Meanders often fold back on themselves, occasionally forming filaments (e.g., Fig. 2), or break, shedding eddies. Combined with southerly winds, filaments moving along and off the shelf break draw deeper, 18 to 22°C, Gulf Stream water up the slope to the shelf break (Blanton, 1971; Pietrafesa et al., 1985a). Domes of 18 to 22°C water within the concave, cold core cusps of filaments are pushed onto the shelf if the wind backs to the north (Pietrafesa, 1989). In winter, cyclonic storm events produce such changing wind fields every 14 days or less (Cione et al., 1993; Pietrafesa et al., in press). Disintegration of remnant filaments stranded on the outer shelf (Lee et al., 1989) through vertical and horizontal mixing (Oey, 1986) can also account for some of the 18 to 22°C water.

Meanders and filaments not only produce this band of 18 to 22°C water on the outer shelf, they also influence the width of this band. Small meanders oscillate closer to shore along the shelf break and compress this band of water; large meanders oscillate farther off the shelf break and stretch this band (Lee et al., 1989). Off Onslow Bay, filaments and meanders, ranging from 10 to 100 km in amplitude, can project almost to the beach (Pietrafesa et al., 1985a), forcing 18 to 22°C water shoreward (Lee et al., 1991) and translocating biota embedded within (Pietrafesa et al., 1988; Tester et al., 1991). Atmospherically driven buoyancy flux on the shelf can also draw this band of water shoreward resulting in the translocation of biota (Miller et al., 1982; Checkley et al., 1988). In the reciprocal, filaments can calve Carolina Capes water into the Gulf Stream as described by Churchill and Cornillon (1991).

Onslow Bay is an area of enhanced exchange between water masses through mixing and stirring. Similarities in temperature and salinity between Carolina Capes and Gulf Stream waters and the cross-shelf tidal vectors (Pietrafesa et al., 1985b) are conducive to mixing (Pietrafesa et al., 1985a). Subtidal currents set



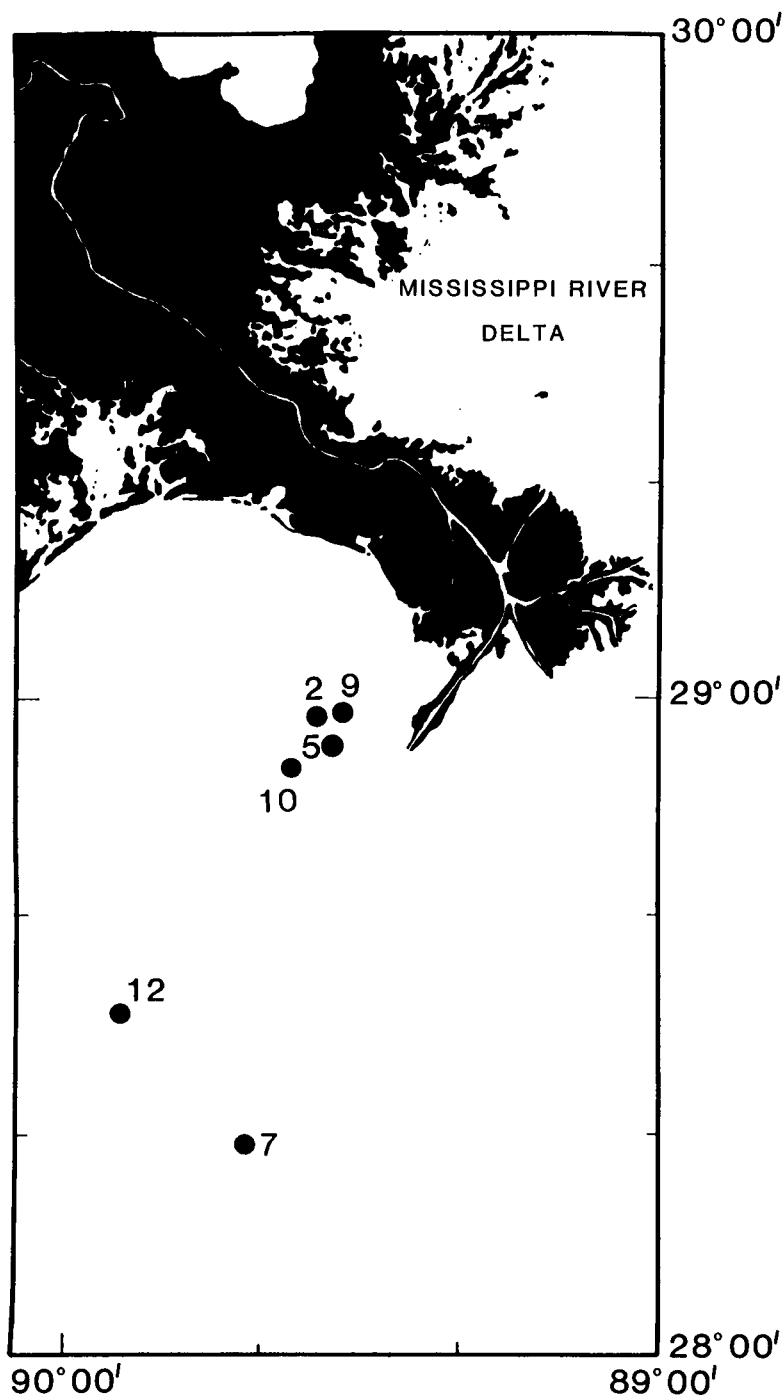


Figure 3. Collection locations of larval *Brevoortia patronus* and *Leiostomus xanthurus* in the northern Gulf of Mexico, December 1982.

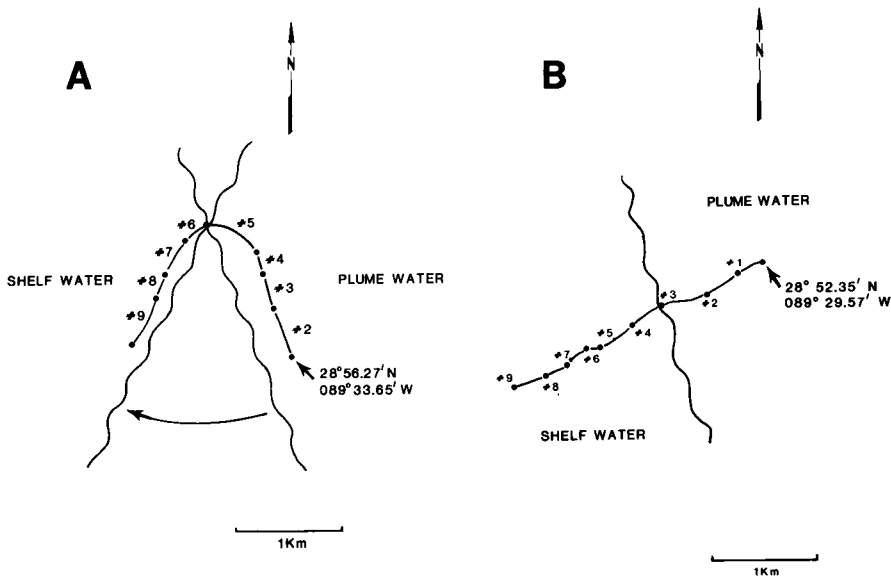


Figure 4. Vessel course and serial net collections made parallel to (A) and intersecting (B) turbidity discontinuities within the Mississippi River plume frontal zone on 24 November 1983. Numbers refer to serial ichthyoplankton collections. The arrow in A) depicts the Lagrangian shift in the axis of the turbidity discontinuity through time.

water on the inner shelf to the south in winter, while water on the outer shelf sets toward the northeast (Stefánsson et al., 1971; Bumpus, 1973). Flux of nutrients and phytoplankton at the inshore margin of the 18 to 22°C band of water is onshore (Ishizaka, 1990; Lee et al., 1991), whereas flux is offshore at the Gulf Stream front (Ishizaka, 1990). The result of mixing and stirring in Onslow Bay is that particles experience a residence time on the outer shelf of from 2 (Blanton and Pietrafesa, 1978) to 3 months (Atkinson et al., 1978), unless caught within filaments and eddies, when they are rapidly advected northward, their residence time lowered to 4 to 6 d (Ishizaka and Hofmann, 1988). Particles introduced onto the shelf through upwelling experience 20-d residence times (Ishizaka and Hofmann, 1988).

#### METHODS OF OBSERVATION

Flux of larval *B. patronus*, *B. tyrannus*, and *L. xanthurus* was addressed by re-examining data from Govoni et al. (1989) for the Mississippi River plume front in the northern Gulf of Mexico and by examining new data for the western Gulf Stream front in Onslow Bay in the northern reaches of the southeastern Atlantic bight of the United States. Because of their association with the two frontal zones, *B. patronus*, *B. tyrannus*, and *L. xanthurus* were taken as indicators of frontal zone water.

In the Gulf of Mexico, ichthyoplankton collections examined were taken in December 1982 and November 1983 with a 1-m MOCNESS (Wiebe et al., 1976), equipped with 333- $\mu$ m mesh nets. Collections taken along a transect from offshore to inshore that intersected the Mississippi River plume front from 5 to 9 December 1982 were examined as an example of large scale distribution (Fig. 3). Along this transect, collections within the body of the plume, or offshore of the plume, were taken obliquely through equally proportioned depth strata of the entire water column. Collections in proximity of the plume frontal interface, as indicated by small scale discontinuities in temperature, salinity, and turbidity (Fig. 1), were taken at the surface either parallel to or intersecting the plume front. The physical structure of the water column was reconstructed from temperature and salinity records taken from MOCNESS casts.

To examine mixing and stirring within the plume front further, the small scale spatial variation in

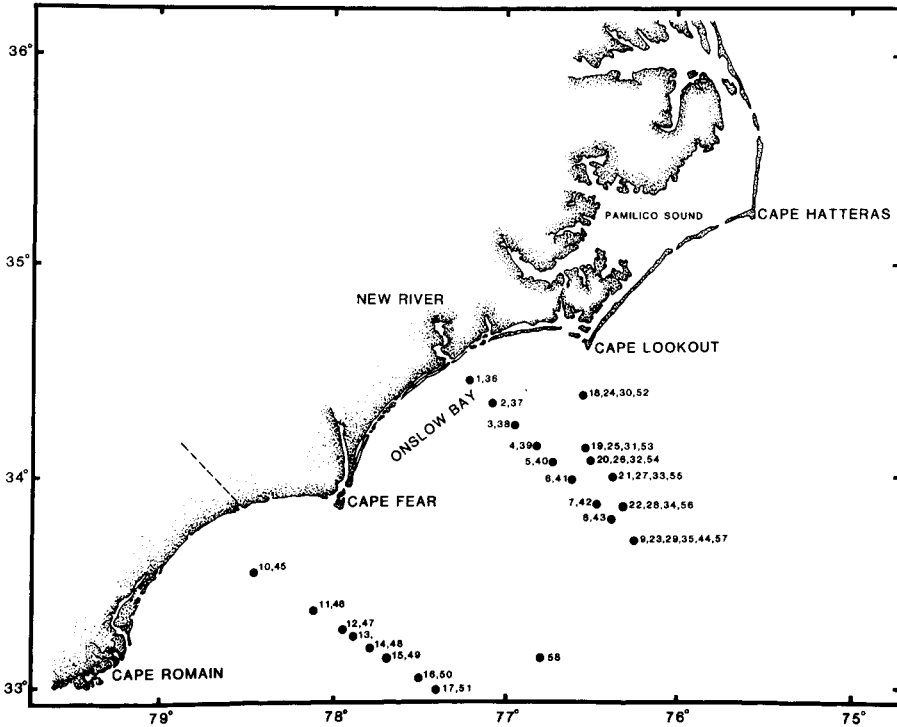


Figure 5. Collection locations of larval *Brevoortia tyrannus* and *Leiostomus xanthurus* in the south-eastern Atlantic Bight of the United States, January and February 1990 and February 1991.

the physical environment and in the distribution of fish larvae was examined in surface collections from two MOCNESS casts made in November 1983. The serial nets of the MOCNESS were opened and closed sequentially along two courses, one that paralleled each side of the plume front and one that intersected the front (Fig. 4).

In the southeastern Atlantic bight, ichthyoplankton collections were taken along three transects in Onslow Bay from offshore within the Gulf Stream to near shore in January and February 1990 and February 1991 (Fig. 5). Collections were taken with either a Tucker Trawl (Clarke, 1969) or standard 60-cm bongo nets (Smith and Richardson, 1977), both equipped with 333- $\mu$ m mesh nets. The physical structure of the water column was reconstructed from temperature and salinity profiles obtained with an Applied Microsystems LTD, temperature, salinity, and depth recorder. The Tucker Trawl was operated obliquely with one net sampling from the surface to the maximum depth sampled, the second sampling deep water, and the third sampling shallow water. Over the shelf, the second net sampled from near bottom to midwater, the third from midwater to the surface. Off the shelf, the second net sampled obliquely through strata with water temperatures roughly 18 to 23°C; the third net sampled the remainder of the water column to the surface. Approximately 16 h elapsed in the occupation of stations along each transect.

Advanced, very high resolution radiometer infrared images from NOAA-10 and NOAA-11 satellites were used in addition by hydrographic sections to determine the horizontal physical structure of continental shelf and upper slope waters. Temperature scales on these images are relative, not absolute, and images were not absolutely synoptic with the occupation of transects.

#### OBSERVATIONS OF LARVAL FISH FLUX

*Cross-Shelf Distribution of Indicator Species in the Northern Gulf of Mexico.*— Across the continental shelf of the northern Gulf of Mexico, larval *B. patronus* and *L. xanthurus* larvae are more abundant in the upper water column, with densities higher inshore than they are offshore (Sogard et al., 1987; Cowan and

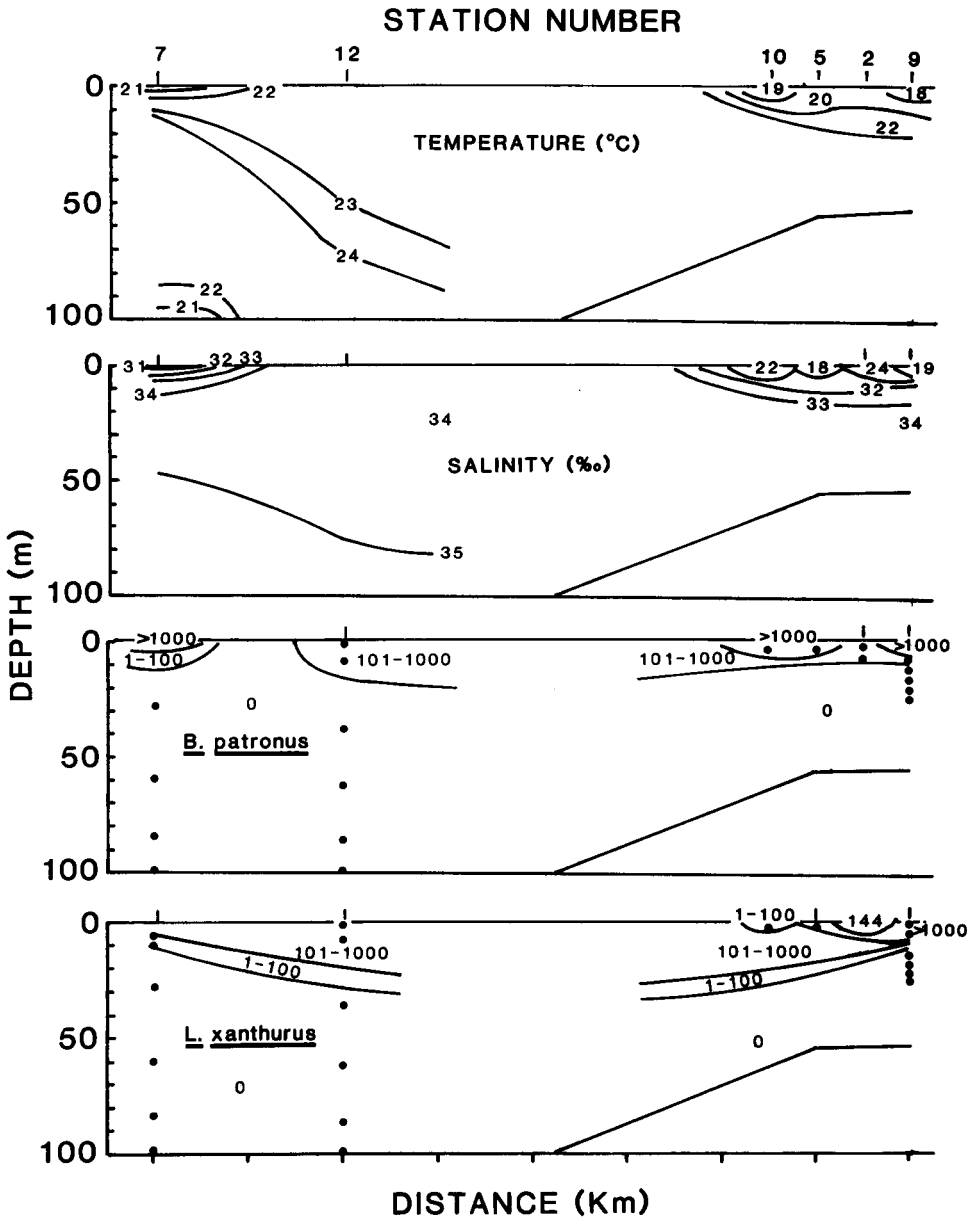


Figure 6. Cross-shelf temperature and salinity sections, and the densities of larval *Brevoortia patronus* and *Leiostomus xanthurus* in the northern Gulf of Mexico, December 1982. Each interval on the horizontal axis represents 1 km.

Shaw, 1988; Shaw and Drullinger, 1990). Ample evidence indicates that highest densities of larvae are observed within the broad scale Mississippi River plume front (Grimes and Finucane, 1991; Govoni and Grimes, 1992), often along temperature, salinity, and turbidity discontinuities (Govoni et al., 1989). High densities of larvae within the frontal zone are best explained by accumulation of

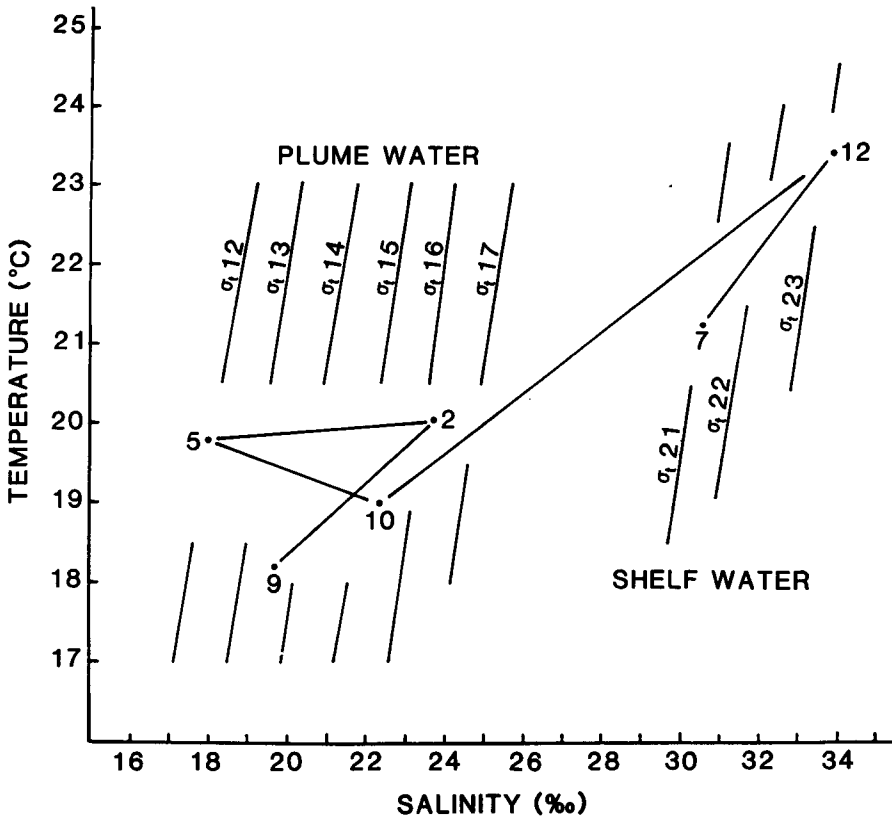


Figure 7. Cross-shelf T/S diagram of surface water in the northern Gulf of Mexico, December 1982.

larvae as the result of convergence (Govoni et al., 1989; Govoni and Grimes, 1992).

Overall, the large scale distributional pattern of larval *B. patronus* and *L. xanthurus*, evident in December 1982 along a transect from offshore to near the Mississippi Delta, conformed with the literature; larvae were more abundant inshore than offshore (Fig. 6). Two high density patches of larvae were evident; one within the plume front, another within the body of the plume. Another high density patch of larval *B. patronus* occurred away from the plume over the shelf.

Mixing and stirring are the most parsimonious explanations of the observed distribution of larvae. At large scales ( $>1$  km), the calving of plume water into shelf water through stirring was evident in the singular and isolated high density of larval *B. patronus* on the shelf away from the plume (station 7, Fig. 6). This exceptional density was associated with a parcel of water apparently detached from the plume front by advective stirring. The T/S signature of this water type falls off a line between those of plume and frontal zone water (stations 2, 5, 9, and 10) and shelf water (station 12) indicating stirring and subsequent mixing (Fig. 7). Corroborative evidence of stirring in the form of detached parcels of water from the plume front also are provided by Govoni and Grimes (1992; Fig. 4A).

The presence of larval *B. patronus* and *L. xanthurus* within the body of the plume (stations 2, 5, 9; Fig. 6) can be explained only by mixing and stirring,

Table 1. Temperature, salinity, and densities of larval *Brevoortia patronus* and *Leiostomus xanthurus* along a turbidity discontinuity within the Mississippi River plume front at 28°56'N/89°33'W on 24 November 1983. MOCNESS net numbers 2 through 5 sampled plume water; 6 through 9 sampled shelf waters (see Fig. 5A for sampling configuration)

MOCNESS net number	Temperature (°C)	Salinity (‰)	Density (number × 10 <sup>3</sup> ·m <sup>-3</sup> )	
			<i>B. patronus</i>	<i>L. xanthurus</i>
Plume side				
2	19.8	25.5	74	0
3	20.1	27.5	446	0
4	19.7	26.4	383	0
5	20.3	28.1	807	0
Mean	20.0	26.8	427	0
Variance	0.28	1.16	300.7	0
Shelf side				
6	20.9	29.5	1,786	0
7	20.9	29.5	2,548	29
8	20.9	29.5	1,867	19
9	20.9	29.5	21,260	19
Mean	20.9	29.5	6,865	17
Variance	0	0	9,602.6	12.1

because all evidence indicates that these species do not spawn in association with the plume or its frontal zone. The mixing processes that probably operate in the Mississippi River plume front are well described by Garvine and Monk (1974). Except in periods of strong wind, turbulent mixing is generated largely by internal shear that results in vertical entrainment (Svendsen, 1986), just as it is in stratified estuaries (Fortier and Leggett, 1982). From station to station within the plume (Fig. 6), the heat and salt content of surface water, as well as densities of larval fishes, varied considerably (Figs. 6, 7). Packets of larvae occurred in parcels of

Table 2. Temperature, salinity, and densities of larval *Brevoortia patronus* and *Leiostomus xanthurus* across a turbidity discontinuity within the Mississippi River plume front at 28°52'N/89°31'W on 26 November 1983. MOCNESS net numbers 1 through 3 sampled plume water; 4 through 9 sampled shelf waters (see Fig. 5B for sampling configuration)

MOCNESS net number	Temperature (°C)	Salinity (‰)	Density (number × 10 <sup>3</sup> ·m <sup>-3</sup> )	
			<i>B. patronus</i>	<i>L. xanthurus</i>
Plume side				
1	19.9	24.9	19,050	4,024
2	20.0	25.3	8,374	2,945
3	20.1	26.0	1,233	2,800
Mean	20.0	25.4	9,552	3,256
Variance	0.10	0.56	8,966.8	668.8
Shelf side				
4	20.4	27.9	5,505	1,971
5	20.4	27.9	644	10,130
6	20.4	27.9	275	4,814
7	20.4	27.8	709	11,200
8	20.4	27.7	6,899	1,220
9	20.4	27.7	837	1,288
Mean	20.4	27.8	2,478	5,104
Variance	0	0.10	2,923.9	4,516.0

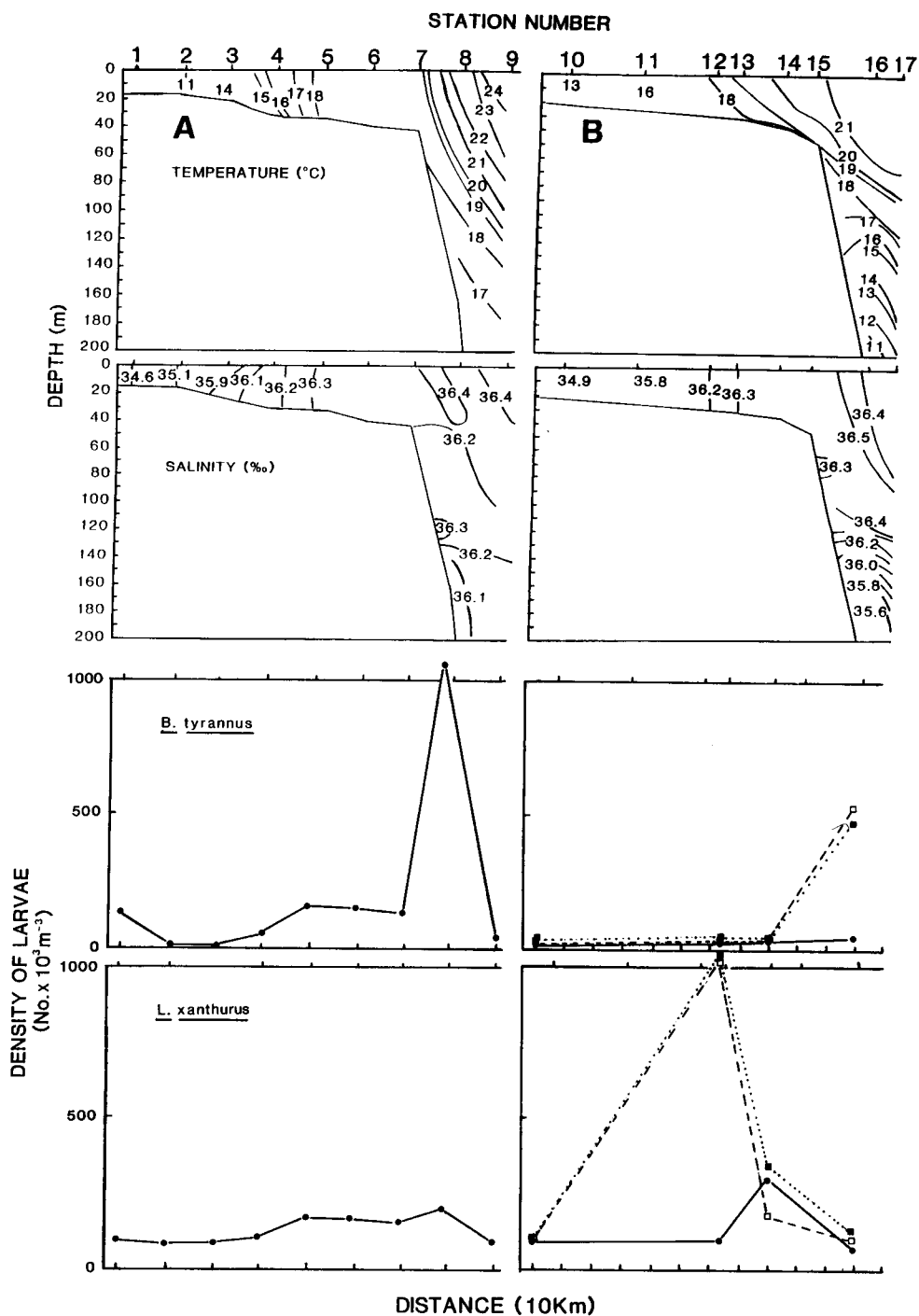


Figure 8. Cross-shelf temperature and salinity sections, and the densities of larval *Brevoortia tyrannus* and *Leiostomus xanthurus* in the southeastern Atlantic bight of the United States. (A) New River transect, 30 January 1990 (oblique bongo-net collections); (B) Cape Fear transect, 1 February 1990 (closed squares, density estimates from Tucker trawl nets that operated obliquely; closed circles, densities from deepwater nets; open squares, densities from shallow water). Each interval on the horizontal axis represents 10 km.

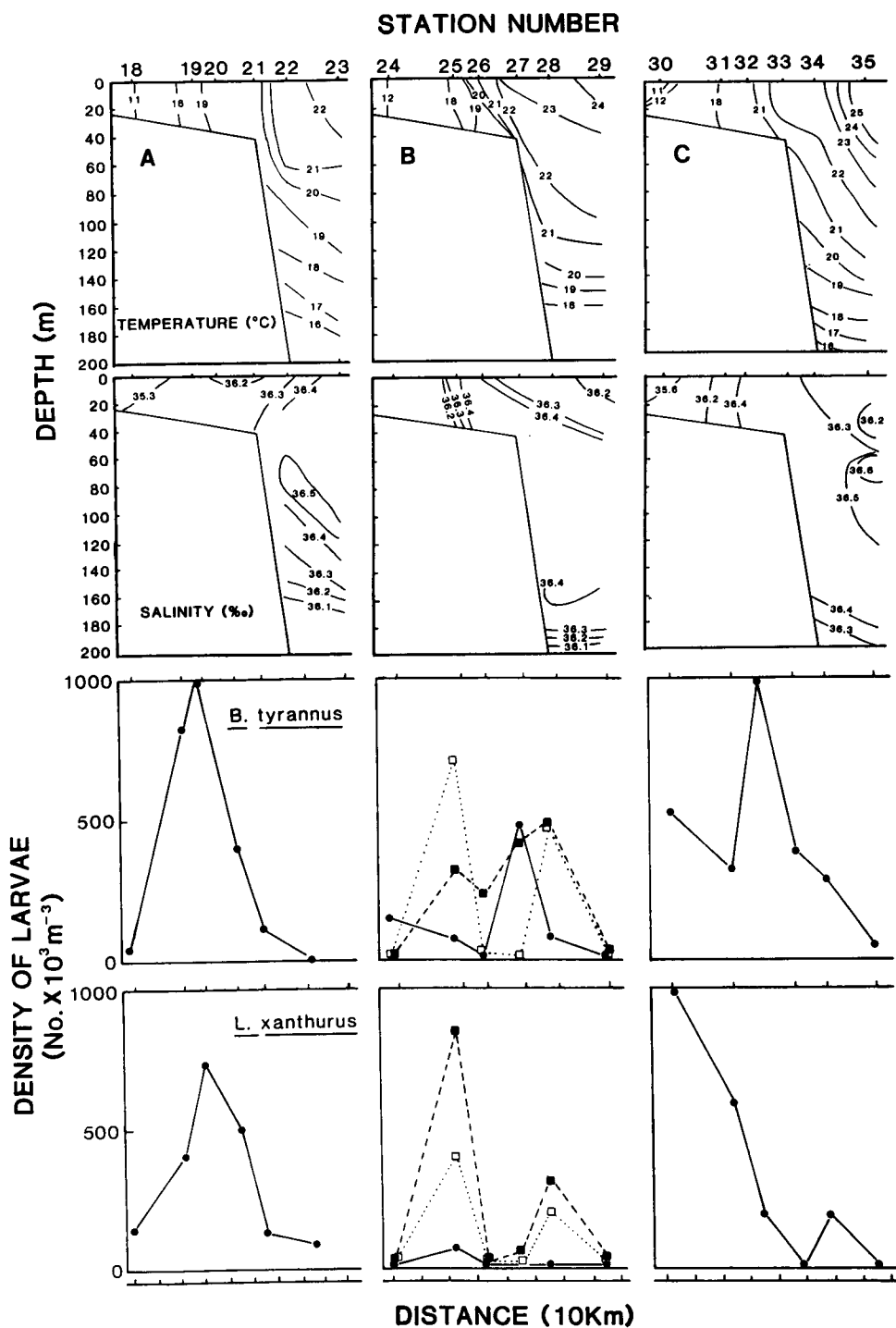


Figure 9. Cross-shelf temperature and salinity sections, and the densities of larval *Brevoortia tyrannus* and *Leiostomus xanthurus* in the southeastern Atlantic bight of the United States. (A) Cape Lookout transect, 27 to 28 January 1990 (oblique bongo-net collections); (B) Cape Lookout transect, 2 February 1990 (closed squares, density estimates from Tucker trawl nets that operated obliquely; closed circles, densities from deepwater nets; open squares, densities from shallow water); (C) Cape Lookout transect, 3 to 4 February 1990 (oblique bongo-net collections). Each interval on the horizontal axis represents 10 km.



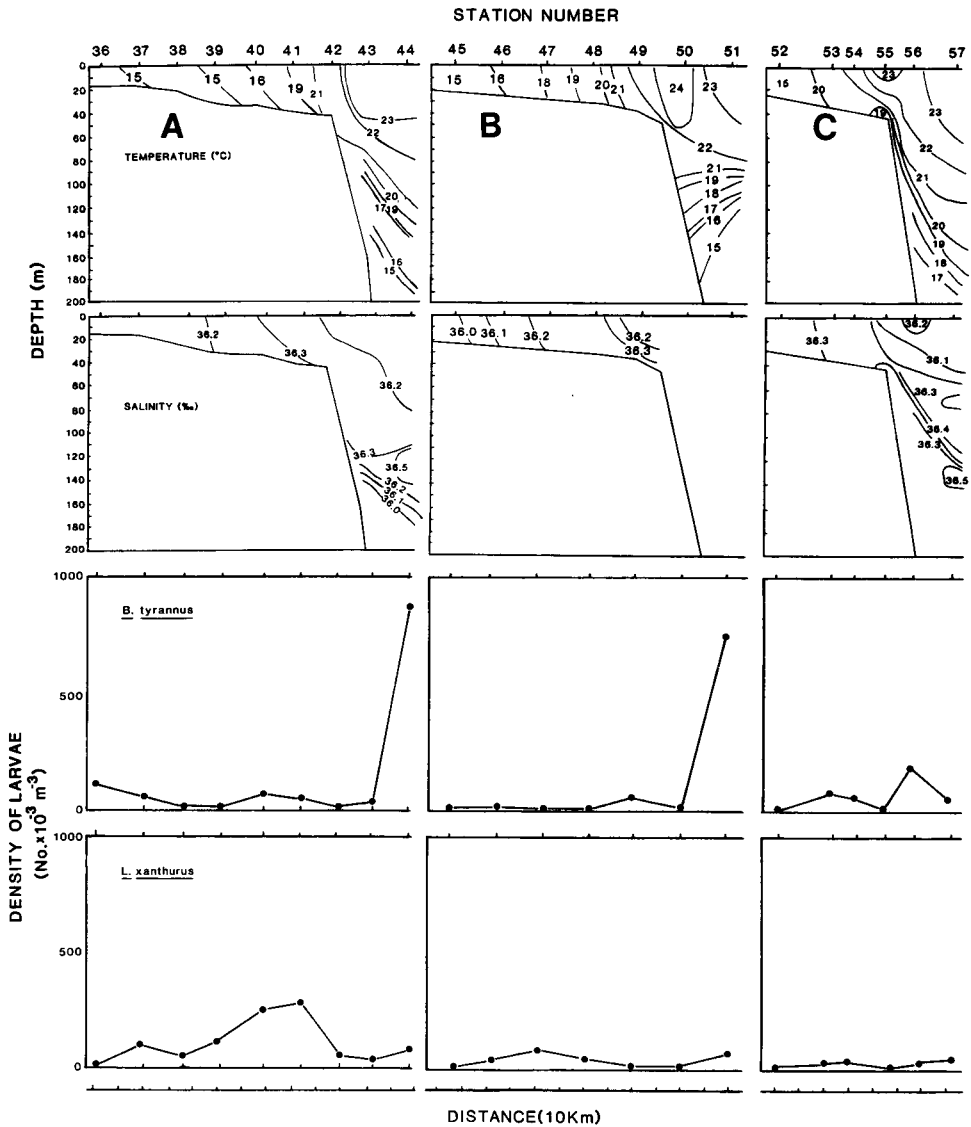


Figure 10. Cross-shelf temperature and salinity sections, and the densities of larval *Brevoortia tyrannus* and *Leiostomus xanthurus* in the southeastern Atlantic bight of the United States (oblique bongo-net collections). (A) New River transect, 7 February 1991; (B) Cape Fear transect, 8 to 9 February 1991; (C) Cape Lookout transect, 10 to 11 February 1991. Each interval on the horizontal axis represents 10 km.

water. The nonlinear variation in temperature and salinity from station to station implies the action of stirring (Tomczak, 1981).

At small scales (<1 km), along and across turbidity discontinuities within the frontal zone (Fig. 4), temperature and salinity on the shelf side of the discontinuity varied little, while within the plume, temperature varied by 1°C and salinity by as much as 2‰ (Tables 1, 2). Parcels of warm, salty water occurred among cool, brackish water. The effects of stirring were seen in the small scale variation in the densities of larvae. At the specific location and time of the sample series taken

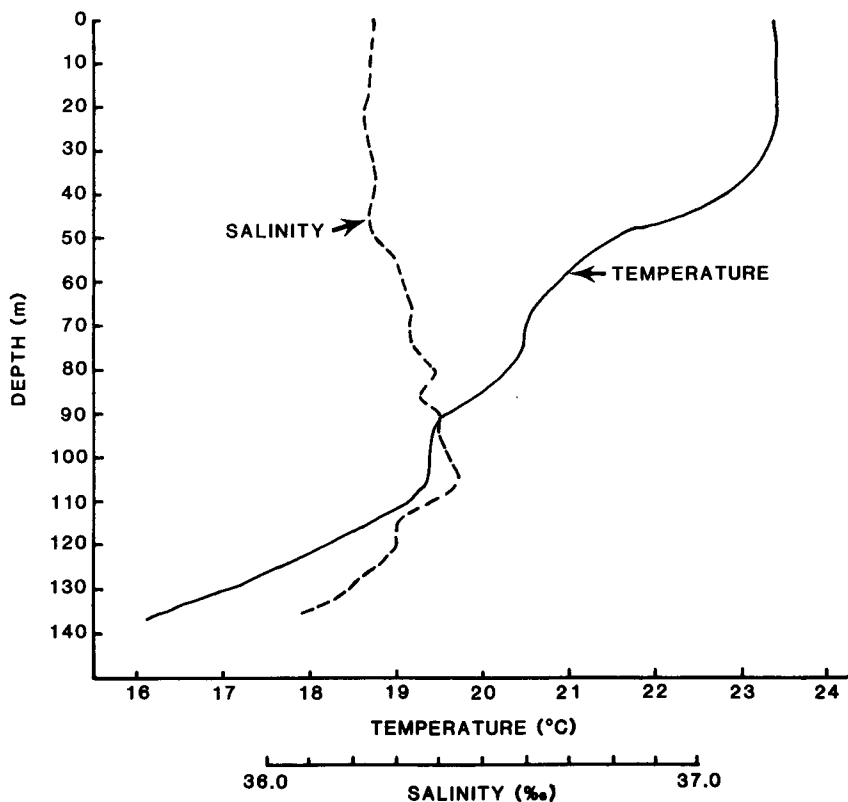


Figure 11. Temperature and salinity profiles within the Gulf Stream at station 58 (33°13.02'N/76°50.14'W) in January 1990.

along a turbidity discontinuity (Table 1), densities of larvae were higher on the shelf-water side of the turbidity discontinuity than on the plume side; densities of larval *B. patronus* within either side varied by an order of magnitude. At another location and time (Table 2), however, densities of larval *B. patronus* were, on average, greater within the plume with the highest density observed almost a kilometer within the body of the plume; densities of *L. xanthurus* were greater on the shelf-water side of the discontinuity. Again, densities varied by a factor of 10. Stirring does not explain the lack of conformity in densities of *B. patronus* and *L. xanthurus*. The larvae of these two species were not associated.

Dramatic indication of flux was evidenced by the presence of the larvae of some deep-sea, mesopelagic fishes within the Mississippi River plume. Argentinoid, stomiatoid, and myctophiform larvae were occasionally collected in shelf waters in the vicinity of the plume, but on two occasions *Bathylagus* sp. and *Bathophilus* sp. larvae were collected at the surface within the body of the plume during the day. These collections (in December and February 1982; Govoni et al., 1989) were taken in MOCNESS casts that paralleled turbidity discontinuities within the frontal zone in the manner illustrated in Figure 5.

*Cross-Shelf Distribution of Indicator Species in Onslow Bay.*—In the southeastern Atlantic Bight, larval fishes typically are in greatest abundance during winter on the outer continental shelf (Yoder, 1983). The larvae of *B. tyrannus* and *L. xanthurus* are abundant across the shelf (Powles and Stender, 1976), overlapping in their eastern distribution with some Gulf Stream inhabitants (Fahay, 1975).

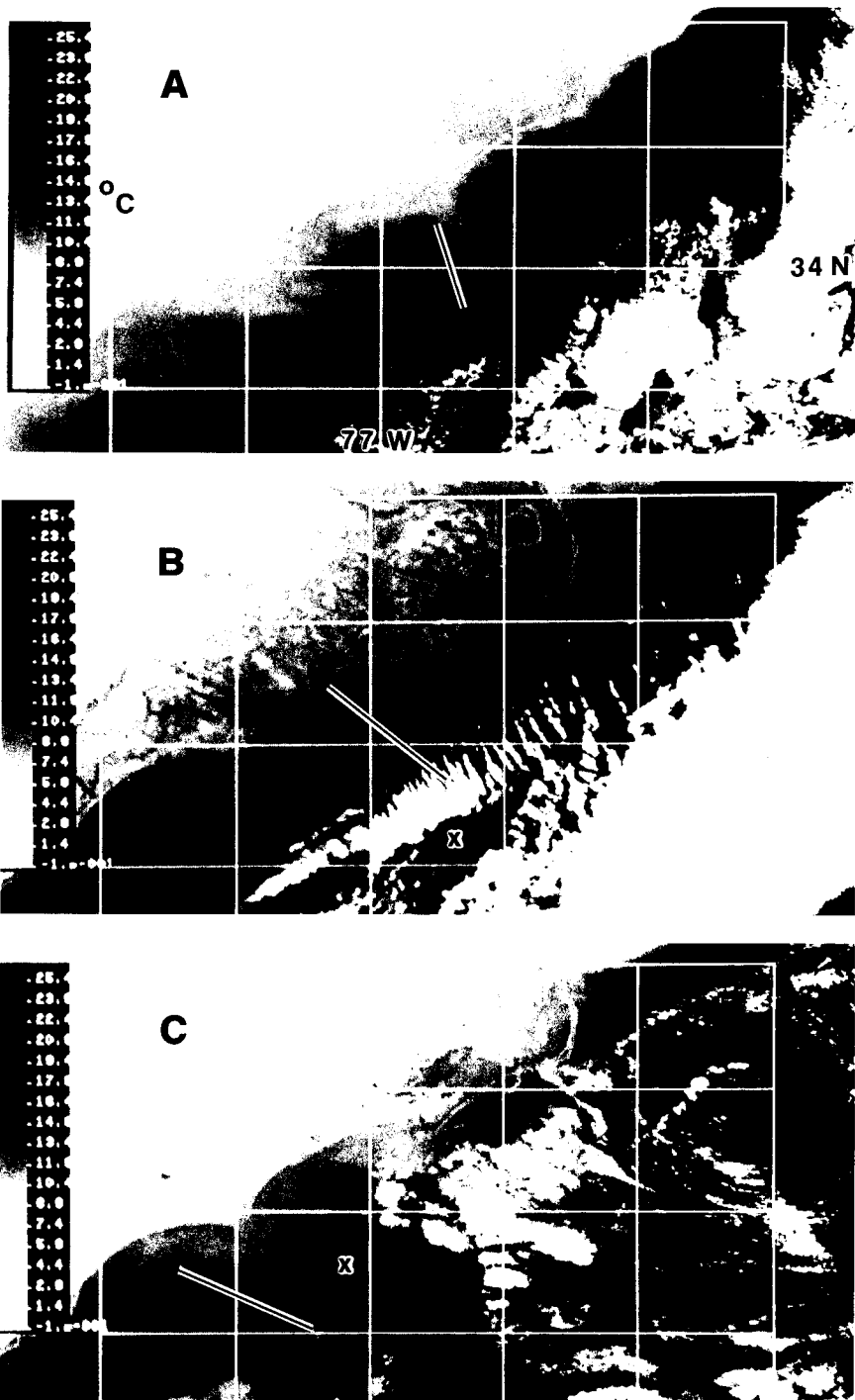


Figure 12. Advanced, very high resolution radiometer infrared image of the Gulf Stream (white areas are cloud cover). (A) 27 January 1990 (NOAA-10 satellite; the line indicates the Cape Lookout transect; (B) 30 January 1990 (NOAA-11 satellite; the line indicates the New River transect, the  $\times$  lies over warm Gulf Stream water, showing through a break in cloud cover); (C) 1 February 1990 (NOAA-11 satellite; the line indicates the Cape Fear transect; the  $\times$ , the cold-core of a Gulf Stream filament).

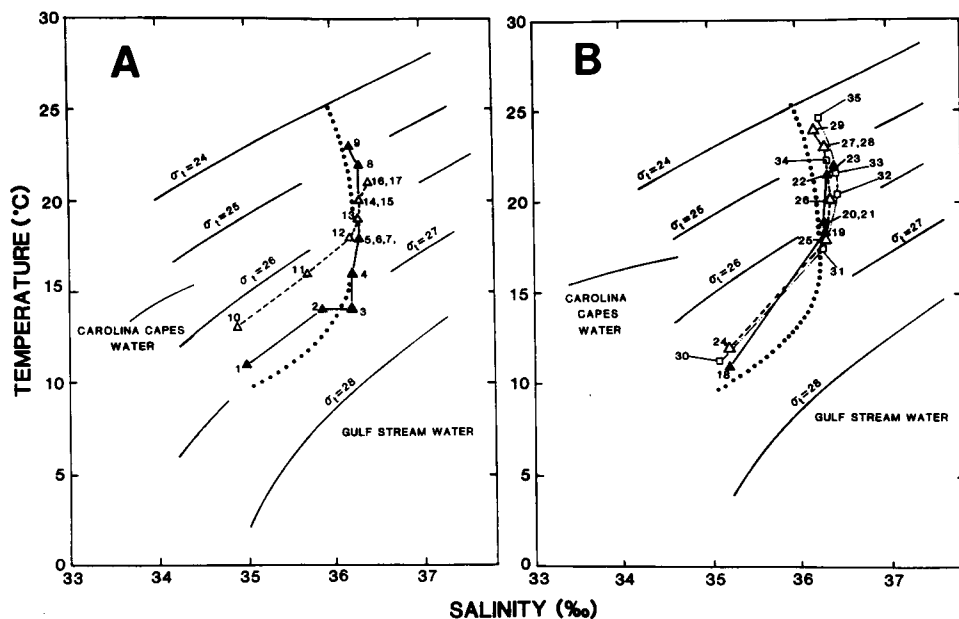


Figure 13. Cross-shelf T/S diagram of surface water in Onslow Bay (dotted line delimits Gulf Stream water as defined by Atkinson [1985] and Pietrafesa et al. [1985a]). (A) New River transect, 30 January 1990 (closed triangles) and Cape Fear transect, 1 February 1990 (open triangles); (B) Cape Lookout transect, 27 to 28 January 1990 (closed triangles), 2 February 1990 (open triangles), and 3 to 4 February 1990 (open squares).

In Onslow Bay, larval *B. tyrannus* and *L. xanthurus* occurred across the shelf, but overall, peak densities within each transect occurred over the outer shelf and shelf break in water of 18 to 22°C (Figs. 8, 9, and 10). Along six of the eight transects (Figs. 8A, B; 9A, B, C; 10C), larval *B. tyrannus* were most abundant within water of this temperature range, usually near or within the outer-shelf or the Gulf Stream fronts. Peak densities of larval *B. tyrannus* along transects occurred in 23°C Gulf Stream water on four occasions; the Cape Lookout transect on 2 February 1990, where a secondary peak of a bimodal distribution was evident, the New River transect on 7 February 1991 (Fig. 10A), the Cape Fear transect on 8 and 9 February 1991 (Fig. 10B), and at an isolated station (station 58, Fig. 5). The greatest density of larval *B. tyrannus* observed in this study,  $7,455 \times 10^3 \cdot \text{m}^{-3}$ , was in a Tucker-trawl collection in the upper water column above the 22°C isotherm (Fig. 11) at this isolated station.

The distribution of *L. xanthurus* conformed generally with the distributional pattern of *B. tyrannus* along four of the eight transects (Figs. 8A; 9A, B; 10A). Along two transects (Figs. 8B, 9C), the cross-shelf distributional pattern of larval *L. xanthurus* departed from that of *B. tyrannus*. On 1 February 1991 along the Cape Fear transect (Fig. 8B), the peak density of larval *L. xanthurus* was inshore of the peak for *B. tyrannus*, but was within the band of 18 to 22°C water. Another exception was the high density of larval *L. xanthurus* in cold (11 to 12°C) water inshore near Cape Lookout on 3 and 4 February 1990 (Fig. 9C). Densities of larval *L. xanthurus* had no obvious pattern, but were uniformly low across the shelf from 8 to 11 February 1991 along the Cape Fear and Cape Lookout transects (Fig. 10B, C).

Spawning within the band of warm (18 to 22°C), salty water upwelled from

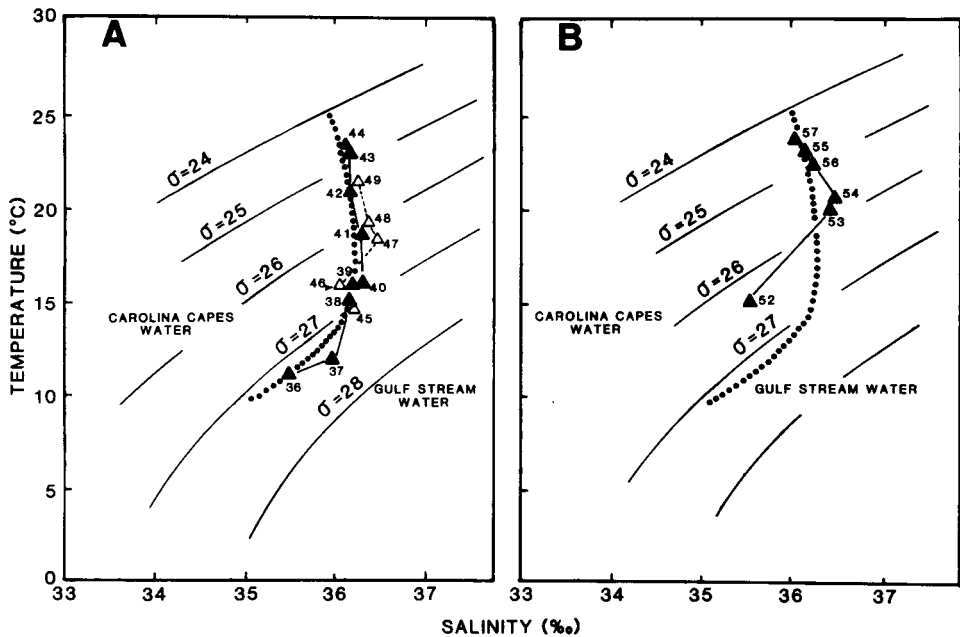


Figure 14. Cross-shelf T/S diagram of surface water in Onslow Bay (dotted line delimits Gulf Stream water as defined by Atkinson [1985] and Pietrafesa et al. [1985a]). (A) New River transect, 7 February 1991 (closed triangles) and Cape Fear transect, 8 to 9 February 1991 (open triangles); (B) Cape Lookout transect, 10 to 11 February 1991.

mid-depth beneath the Gulf Stream front probably accounts for the greater abundance of larvae over the outer shelf and shelf break. Domed isopleths on the continental slope off Cape Fear in 1990 and 1991, and Cape Lookout in 1991 indicate upwelling activity that typically accounts for the presence of this water on the outer shelf (Figs. 8B; 10B, C). A ridge of cool upwelled water at the surface was evident in a filament cusp that passed the offshore reach of the Cape Lookout transect on 27 January 1990 (Fig. 12A). Another ridge was apparent to the southeast of the New River transect on 30 January 1990 (Fig. 12B). A well defined dome of cool water at the surface, also associated with a filament cusp, was apparent on 1 February 1990 (Fig. 12C).

Mixing can explain the presence of larval *B. tyrannus* and *L. xanthurus* on the shelf inshore of the outer-shelf and Gulf Stream fronts. Ascending T/S signatures of water types across the inner and middle shelf along the New River and Cape Fear transects (Fig. 13A) indicate mixing of nearshore water and Gulf Stream water. Mixing of this sort accounts for the physical properties of Carolina Capes water (Pietrafesa et al., 1985a). Mixing was not as apparent along the Cape Lookout transect, where the shelf is narrow and the Gulf Stream closer to shore (Fig. 13B). While the Gulf Stream front was on the shelf in January and February of 1991 (Fig. 14A), its integrity was apparent in the sharp inflection of signatures on the outer shelf, where surface temperatures and salinities rose sharply in Gulf Stream water (Figs. 13B, 14B).

Stirring, in the form of Gulf-Stream meanders and filaments, can translocate larval *B. tyrannus* and *L. xanthurus*. Along the Cape Lookout transect from 27 January to 4 February 1990, the outer-shelf and Gulf Stream fronts were separated, merged, then separated again (Fig. 9), the sort of dynamic activity that typically

results from the action of Gulf Stream meanders or filaments. The bimodal distribution in peak densities (Fig. 9B) may have been caused by filament passage. One peak occurred within the outer-shelf front, the other in 23°C water in the Gulf Stream near its front. The presence of a filament was not apparent in the cross-shelf temperature and salinity sections (cloud cover obscured a view of this transect from space), but a filament was observed to the south on 1 February 1990 (Fig. 12C). This filament would have propagated past the Cape Lookout transect by 2 February 1990, compressing the band of the 18 to 22°C water at the shelf break and leaving in its wake a deformation in the distribution of larvae. More convincing evidence of the effect of meanders and filaments was seen along the Cape Fear and Cape Lookout transects 8 to 11 February 1991 (Figs. 10B, C). The dynamic nature of the Gulf Stream front is clear from the sequence of satellite images of sea-surface temperature that covered these dates (Figs. 15, 16). The Cape Fear transect appeared to have intersected the inner edge of a meander (Fig. 15B). The peak in larval *B. tyrannus* density was within the Gulf Stream, but close by its front (Fig. 10B). Two filaments persisted in the vicinity of the Cape Lookout transect on 10 to 11 February 1991 (Figs. 15C; 16A, B, C). A lens of warm (23°C) surface water over the shelf break was evidence of the filament's tongue, cooler (22°C) surface water over the upper slope indicates the concave inner cusp of the filament, and 23°C water farther off the shelf break is the front of the Gulf Stream proper (Figs. 10B, C). The distribution of densities of larval fishes was bimodal across the shelf break and slope as the filament passed the Cape Lookout transect. One peak occurred in 20°C water inshore of the filament tongue (station 53), the other peak in 22°C water within the filament's cusp, but near the 23°C isotherm (station 56).

#### CONSEQUENCES OF FLUX

There are two principal consequences of the flux of larval fishes across frontal boundaries; transport to areas favorable, or even necessary, for their further development (Miller et al., 1982; Shaw et al., 1985), and dispersal or expatriation (Sinclair, 1987). The positive gradient in the length and age of larval *B. patronus*, *B. tyrannus*, and *L. xanthurus* from offshore to inshore, the presence of juveniles in estuaries, and the absence of juveniles on the continental shelf implies cross-shelf movement, but the mechanism that operates in transporting larvae from the outer continental shelf to estuaries is presently unknown. In the Gulf of Mexico, a current, working hypothesis is that larvae accumulate along frontal zones, the Mississippi River plume front and the coastal boundary front, are entrained into coastal water, and are injected into estuaries with astronomically and meteorologically forced rises in sea level (Shaw et al., 1985; Cowan and Shaw, 1988). In the southeastern Atlantic bight, averaged Ekman transport, once proposed as the sole mechanism (Nelson et al., 1977), is no longer an entirely adequate explanation. Other, more complicated mechanisms probably operate (Miller et al., 1982; Checkley et al., 1988; Hoss et al., 1989), but there are presently no empirical tests of these hypothetical mechanisms. If larvae are trapped within the Mississippi River plume, the outer shelf, or the Gulf Stream frontal zones, or if fronts act as barriers, larvae cannot accomplish shoreward transport. The mechanisms of shoreward transport, whatever they are, require flux of larvae from offshore frontal zones into the coastal zone.

Ingress of *B. patronus*, *B. tyrannus*, and *L. xanthurus* into estuaries is episodic. Pulses in abundances of larvae within inlet passages appear at both short (Lyczkowski-Shultz et al., 1990) and long (Hettler and Chester, 1990; Warlen and Burke,

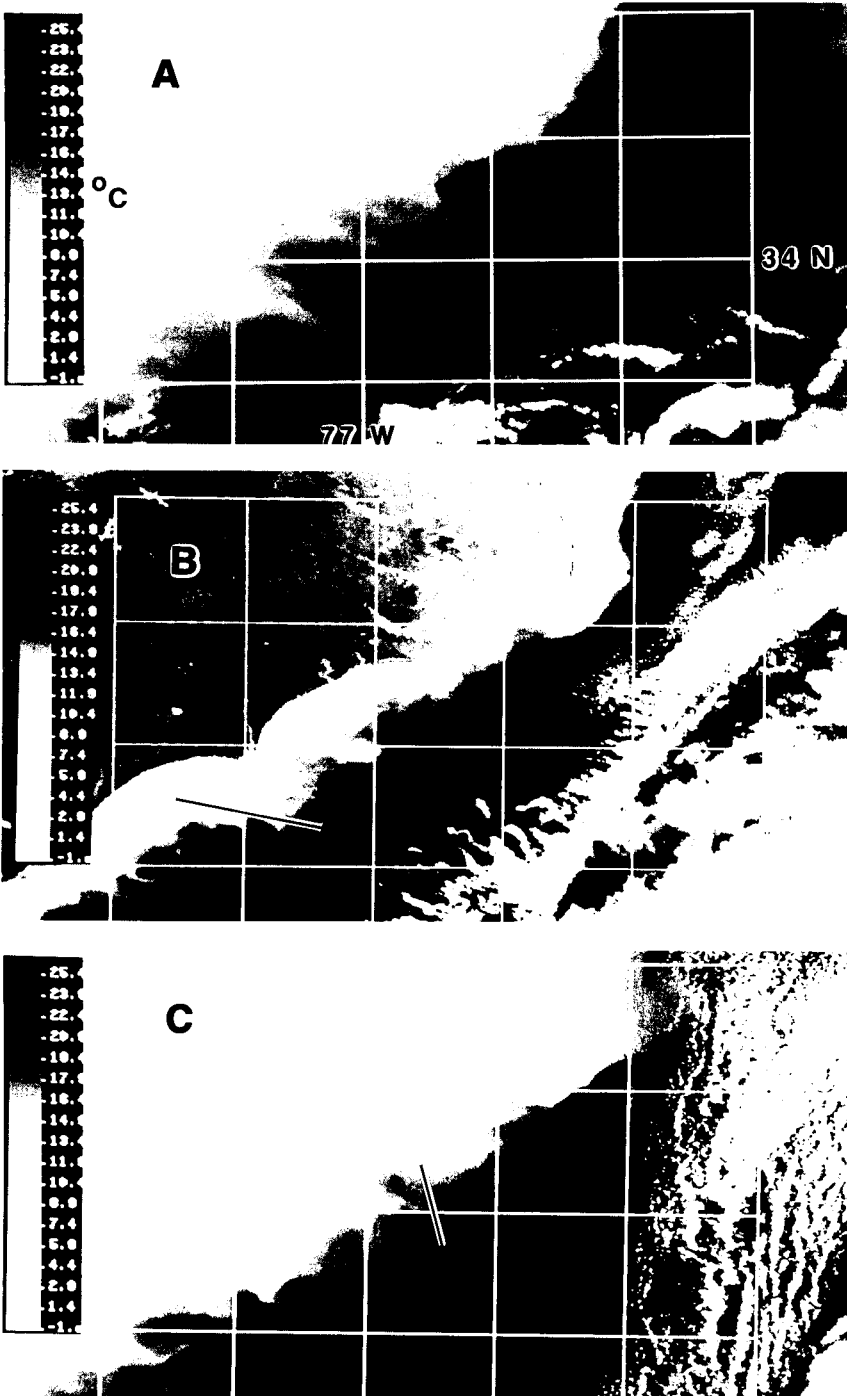


Figure 15. Advanced, very high resolution radiometer infrared image of the Gulf Stream (mottled white areas to the right are clouds). (A) 5 February 1991 (NOAA-10 satellite); (B) 9 February 1991 (NOAA-11 satellite; the line indicates the Cape Fear transect); (C) 10 February 1991 (NOAA-10 satellite; the line indicates the Cape Lookout transect).

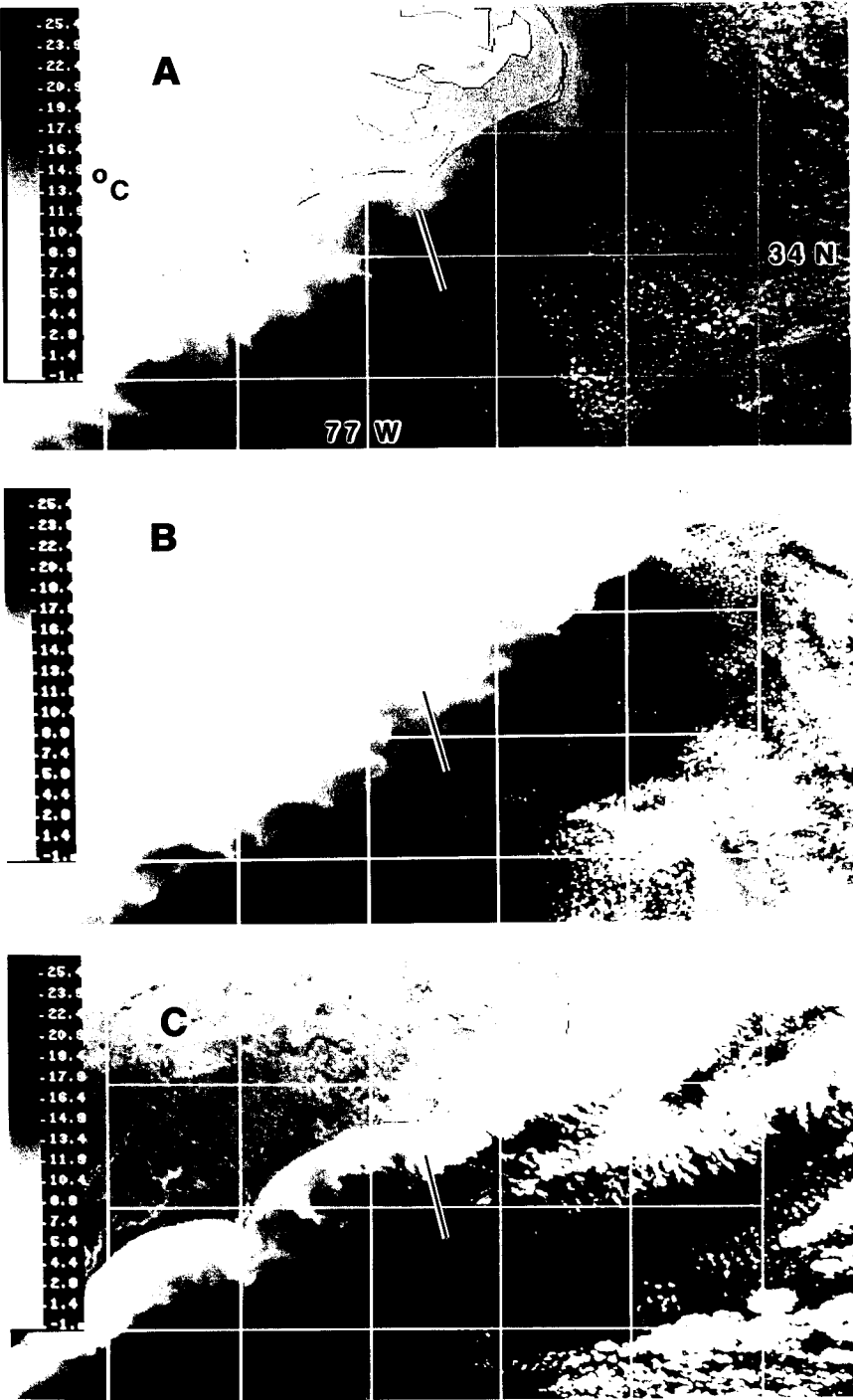


Figure 16. Advanced, very high resolution radiometer infrared image of the Gulf Stream, 11 February 1991 (mottled white areas to the right are clouds, lines indicate Cape Lookout transect). (A) NOAA-11, 0735 h Greenwich Mean Time (GMT); (B) NOAA-10, 1227 h GMT; (C) NOAA-11, 1902 h GMT.



1990) time frequencies. No periodicity in larval fish abundance that is coherent with lunar-tidal cycles is presently evident (Hettler and Chester, 1990; Lyczkowski-Shultz et al., 1990). Estuarine dynamics may produce pulses of larvae within inlets, but another possible cause is the advective flux of larvae in packets across the shelf toward the coast. The present observations, however, lend no evidence of this. Larvae of these species in Carolina Capes water is best explained by mixing.

The reciprocal of shoreward movement, loss of larvae from the shelf, is apparent in the observations of a high density of larval *B. patronus* off the shelf of the northern Gulf of Mexico and of similarly high densities of larval *B. tyrannus* within the Gulf Stream off Onslow Bay. Some expatriation is probable because the existence of larval *B. patronus*, *B. tyrannus*, and *L. xanthurus* brackets the residence time of Mississippi plume water and Carolina Capes water. Expatriation via flux into the Gulf Stream is evident for other species (Govoni and Merriner, 1978; Markle et al., 1980; Wroblewski and Cheney, 1984; McGowan and Richards, 1989). Both transport and expatriation have major impacts on the population dynamics of species (Sinclair, 1987).

The spatial distribution of larval fishes in the vicinity of the Mississippi River plume front in the northern Gulf of Mexico and the Gulf Stream front off Onslow Bay in the western North Atlantic, superimposed on the physical structure of the waters in which these larvae are embedded, illustrates flux of larval fishes across frontal boundaries through the exchange processes of mixing and stirring. Mixing can best account for the presence of the larvae of indicator species in the body of the Mississippi River plume and in Carolina Capes water on the shelf in Onslow Bay. Stirring can account also for parcels of larvae within the Mississippi River plume. The calving of Mississippi plume water into shelf water of the northern Gulf of Mexico is clearly evident. Stirring, in the form of Gulf Stream meanders and filaments, results in deformation of the distribution of the larvae of indicator species along the outer continental shelf in Onslow Bay. Stirring does not account for the presence of the larvae of indicator species in Gulf Stream water. Mixing of 18 to 22°C, i.e., water associated with the outer-shelf and Gulf Stream fronts, with Gulf Stream water south of Onslow Bay is a possibility.

The examples of larval fish flux given, although isolated temporally and geographically, have global relevance. Plume fronts are common to the world's major river outlets (Lohrenz et al., 1990), and western boundary currents all have well defined frontal zones (Owen, 1981).

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